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Maxithermy and the thermal biology of an herbivorous sand dune lizard

R. D. Pietruszka* 1988

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Simultaneous measurements of sand surface temperatures and microsite occupancy across the major activity areas of a sand dune were recorded for the lizard *Angolosaurus skoogi* and compared to expectations of thermally directed patterns of habitat use from the maxithermy hypothesis. Little correspondence was found between the patterns of habitat use and sand surface temperatures, suggesting that *Angolosaurus* does not follow a maxithermal strategy of thermoregulation. Rather, *Angolosaurus* appears to use the sand dune habitat mainly for reasons other than thermal considerations, such as foraging, social interactions, and predator surveillance. The presence of an immediate thermal refuge in the form of subsurface sand is perhaps the principal underlying factor.

Introduction

Within arid environments, sand dunes provide unique habitats that may be simultaneously thermally intolerable and yet be the source of a virtually complete thermal refuge to diurnal ectothermic organisms (Louw & Seely, 1982; Seely 1983). Sand surface temperatures change rapidly, often presenting severe thermal challenges to organisms occupying them (George, 1986). On the other hand, because of the relatively high insulating capacity of sand (Geiger, 1965), the subsurface environment provides an immediate refuge from excessive surface temperatures (Seely & Mitchell, 1986). This marked contrast in the surface and subsurface microenvironments is likely to have a major impact on the thermal biology of diurnal ectotherms occupying sand dune habitats.

One option for sand dwelling animals may be to follow a strategy of maintaining high body temperatures for the maximum possible time during the daily activity period. Under this maxithermy hypothesis (Hamilton, 1971, 1973, 1975), diurnal ectothermic animals use a variety of tactics, particularly thermoregulatory posturing and active microsite selection, to maintain maximum body temperatures. This kind of a strategy allows for higher metabolic rates that presumably result in faster nutrient processing and eventually in higher reproductive rates, which are ultimately postulated to lead to a competitive advantage over other species not following such a strategy (Hamilton, 1971, 1973; Henwood 1975).

Maxithermy

Besides the general expectation that maxithermal species will have relatively stable and high body temperatures, it also follows that space-use will be rather closely tied to maintaining these temperatures. Specifically, the maxithermy hypothesis predicts that those microhabitats which produce the most rapid rise in body temperature will be actively sought out at the beginning of each daily cycle and, thereafter, movement within the thermal mosaic will serve to maintain temperature within a limited, high range (Hamilton, 1973; Henwood, 1975).

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* Desert Ecological Research Unit, P.O. Box 1592, Swakopmund, 9000, SWA/Namibia.

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For the most part, the maxithermy hypothesis has been directed at small ectothermic invertebrates inhabitating desert regions and in particular to the diverse tenebrionid beetle fauna of the Namib Desert of South West Africa/Namibia (Hamilton, 1971, 1973; Henwood, 1975). Among vertebrates, on the other hand, only one lizard, *Angolosaurus skoogi*, also from the Namib, has been specifically highlighted as following a maxithermal strategy (Hamilton & Coetzee, 1969; Hamilton, 1973). *Angolosaurus* is unusual in that it is a predominantly herbivorous species that inhabits the largely vegetationless sand dunes of the northern Namib from approximately the Unjab River northward into Southern Angola (Pietruszka *et al.*, 1986). It is also the largest sand diving lizard species occurring in the Namib sand sea—reaching a total length of up to 30 cm with a mass that may surpass 100 g. These features make *Angolosaurus* intriguing from a thermoregulatory standpoint, especially considering that slipfaces inhabited by these lizards frequently reach surface temperatures in excess of 60°C.

Maxithermy generally has not been considered as an important option in the thermoregulatory behaviour of reptiles (e.g. Huey & Slatkin, 1976). Presumably, at least one reason for this is that under the maxithermy hypothesis such behaviour would almost certainly have to include an important motivational component that is difficult to examine in either field or laboratory settings. Recent evidence, however, suggests that a reptile's familiarity with the environment of its home range may have thermal consequences that closely parallel the expectations of a maxithermal approach to thermoregulation (Chelazzi & Calzolai, 1986). Thus, it is of interest to reconsider one of the more tractable corollaries of maxithermy, that of thermally directed patterns of habitat use, in an animal previously considered to be illustrative of this approach to coping with thermal extremes in an arid environment.

Early ecological work on *Angolosaurus* (Hamilton & Coetzee, 1969) interpreted observations of microhabitat location and posturing as behavioural adjustments that allowed lizards to maintain body temperatures within the 38–42°C range for as long as possible during the active period. Based on limited measurements of sand surface temperatures, these authors also postulated that *Angolosaurus* was selecting specific locations on the dune slipface to take advantage of its thermal mosaic. In this paper I consider the use of microhabitats in relation to simultaneous measurements of environmental temperature and ask whether this may, in fact, reflect a maxithermal strategy.

Study Area

The site for this study was located on the south bank of the normally dry bed of the Unjab River, approximately 12 km inland along the eastern side of the northern Namib dunes (20°, 09′ S, 13° 14′ E) in SWA/Namibia. Sand dunes in this area are primarily barchandoid ridges, 3–10 m in height, with connected concentric slipfaces (Lancaster, 1982). The dominant S to SW winds produce windward slopes of 10–12° and slipfaces of 31–34° slope (Fig. 1). Average maximum daily air temperatures in the area range between 13 and 24°C with minima between 9 and 15°C. Winds capable of moving sand (> 4 m/s) blow for up to 50% of the time (Lancaster, 1982).

Within the study area, the unstable sand surface of the dunes was almost devoid of vegetation. The dominant dune plant was the nara, *Acanthosicyos horrida*, a sparsely distributed, long-lived cucurbit. On the interdune areas some persistent plant species, including *Sueda plumosa*, *Merremia guerichii*, *Sesuvium sesuvioides*, *Zygophyllum simplex*, and several grasses of the genus *Stipagrostis*, were present. Total vegetative cover, however, was $<1\%$ (Pietruszka *et al.*, 1986).

The specific *Angolosaurus* population investigated inhabited a dune averaging about 9·4 m in height, with a total area of approximately 1000 m^2. In cross section, seven distinct areas of *Angolosaurus* activity could be recognized—top, crest, upper, middle, and lower

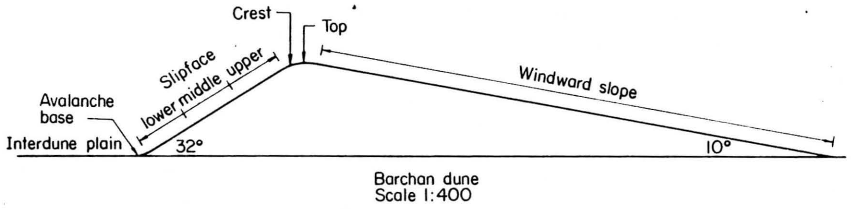

Figure 1. Diagrammatic representation of an Unjab River dune showing the principal *Angolosaurus* activity areas.

slipface, avalanche base, and interdune plains (Fig. 1). In addition, on those dunes having vegetation, such as the one in this study, an eighth area of activity was associated with the vegetation patch.

Methods

Data on microsite usage in relation to sand surface temperatures were obtained using a scan sampling technique (Altmann, 1974). Because these lizards are exceedingly wary, field procedures involved direct observation of active *Angolosaurus* from two portable tents used as hides. From these concealed positions, the entire surface-active population was counted, at 5 min intervals, throughout the day over a 7-day period. During each scan, the location of every lizard was classified into one of seven microsite locations across the dune and lizards were grouped as well into one of six age/sex categories (Table 1). Lizard censuses were conducted by two observers from a hide placed approximately 30 m from the slipface, giving an optimal view of the study area. Observations always began prior to the onset of surface activity in the morning and continued throughout the day until the last individual ceased activity in the evening.

Table 1. *Categories used in activity censuses*

Dune location	Age/sex
Top*	Young
Crest*	Juvenile
Slipface	
upper 1/3*	Adult (females + subadult males)
middle 1/3*	Male
lower 1/3*	Head only
Avalanche base*	Unidentified lizard
Nara	

* Location of thermocouple temperature probe.

Surface temperatures were obtained by means of copper-constantan thermocouples placed on the sand surface within the seven activity areas across the dune and connected to a portable digital thermocouple thermometer fitted with a rotary switch for multiple inputs. Surface temperature was recorded simultaneously with the population censuses by a third observer located in a second hide closer to the study dune. Statistical analyses follow the methods of Conover (1980) and Sokal & Rohlf (1981).

Results and discussion

From previous work in the study area (Mitchell *et al.*, 1988; Seely *et al.*, 1988a) it is known that *Angolosaurus* activity may extend from 4 to 8 h in either bimodal or unimodal bouts depending on prevailing conditions. Not every member of the population is active every day and as little as one third of the population may be surface-active on any given day. When inactive, individual *Angolosaurus* are buried up to 30 cm or more below the sand surface and can remain there for a period of at least 7 days. In the current study, minimum surface temperatures for observed activity range from about 27 to 31 °C, whereas maximum surface temperatures associated with activity may be as high as 61°C.

The patterns of activity during the study, both across the dune and by different age/sex groups, are reflected in the diversity measures shown in Table 2. Two features are apparent. First, age/sex classes within the surface active population are seldom equally represented. The two youngest age classes (young, juvenile) generally dominated daily activity, accounting for 48·9–78·8% of the total daily sightings during the study. This is similar to the range found by Seely *et al.* (1988a), 49·8–68·0%, at another nearby dune and suggests a degree of parallelism among local populations. Second, not all areas of the dune are equally likely to be utilized and the evenness of activity across the dune varies from day to day. During the course of the study, the breadth of microsite usage ranged from a low of only 29·5% of maximum (D_{max}) to just over 64% of D_{max} with an overall variability of almost 27% (Table 2). This pattern suggests that there may indeed be a measure of microsite selection on the dune, perhaps in response to surface temperatures.

Table 2. *Microsite use and age class diversity* ($1/\Sigma p_i^2$)

Day	Dune location	% max (8)	Age/sex class	% max (4)
1	4·18	52·3	3·39	84·8
2	2·36	29·5	2·26	56·5
3	3·46	43·3	2·75	68·8
4	4·90	61·3	3·95	98·8
5	5·15	64·4	2·77	69·3
6	4·40	55·0	2·69	67·3
7	2·98	37·3	2·00	50·0
Average	3·92	49·0	2·83	70·8
CV (%)	26·80		23·31	

% max, D_{max}, gives the per cent of maximum diversity and indicates the evenness of activity across the dune. Numbers in brackets indicate maximum evenness.

An examination of the patterns of surface temperatures within the seven activity areas throughout the day revealed a comparatively limited thermal mosaic on the study dune. In general, at those times during the day when the thermal gradient across the dune was at its greatest, surface temperatures over most of the activity zones appeared excessive for sustained activity. Thus the usable thermal mosaic was, in fact, smaller than might otherwise be expected. At cooler periods during the day the overall gradient diminished. These general patterns are illustrated in Fig. 2. These data depict average surface temperatures across the seven activity zones along with the one standard deviation band during two diurnal periods. Limitation in the surface temperature mosaic is further reflected in the low coefficients of variation (CV) for surface temperatures across the dune, which generally ranged below 10% throughout the diurnal period of activity (Fig. 2).

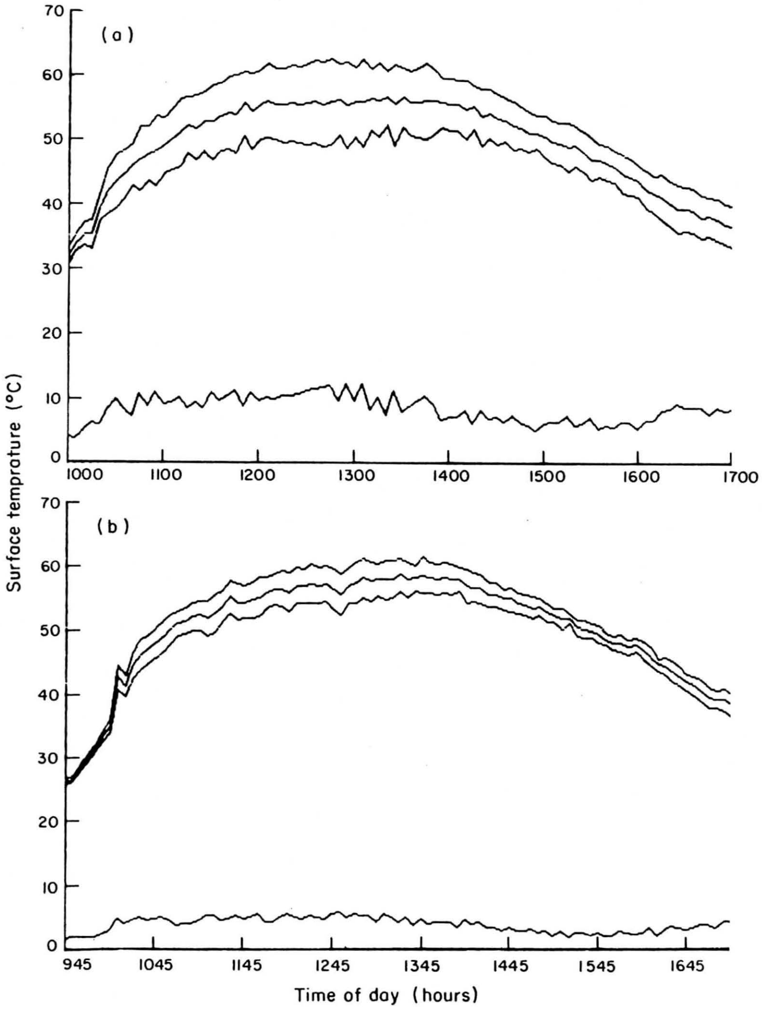

Figure 2. Surface temperature profiles across the seven activity zones of *Angolosaurus* throughout the day during two diurnal activity periods, (*a*) 14 February and (*b*) 18 February 1986. Upper portions of each plot give mean surface temperatures (middle) and one standard deviation band. Lower portions depict the coefficient of variation in surface temperatures across the dune during the day.

Superimposed on diurnal fluctuations in surface temperatures are day-to-day variations in the extent of a thermal mosaic across the dune. The spatial variation in surface temperatures recorded on 14 February 1986 (Fig. 2*a*) was the maximum observed during our 7 days of observation. On this day, the maximum amplitude of temperature difference across the seven activity areas ranged from 17 to 21°C over a period of approximately 2·5 hours. The gradient was considerably reduced 4 days later (Fig. 2*b*), with a maximum temperature amplitude of only 6–7°C over the same time period and maximum CV's of only about 5%. In general, these surface temperature data suggest that if *Angolosaurus* is selecting locations on the dune with respect to thermal microhabitats, it must do so in the face of a rather narrow range of temperatures from which to choose.

If *Angolosaurus* behaves maxithermally, then one would expect (1) movement to those locations on that dune that provide for the most rapid increase in body temperature at the onset of daily activity, and (2) an overall correspondence between the location of surface activity and surface temperature as lizards move through the mosaic in order to maintain high body temperatures. Figure 3 shows plots of hourly census results across the dune along with the average hourly surface temperatures at these locations for three different diurnal activity periods. Inspection of these plots provides insights into the degree to which the above expectations may normally be met by active *Angolosaurus*.

On 14 February 1986 (Fig. 3*a*), emergence occurred between 10:00 and 11:00 local time. During this time, the majority of surface active animals moved immediately to either the dune top or crest, even though remaining on the middle slipface would appear to have produced more rapid rates of heating. Moreover, these locations were the ones most frequently occupied throughout > 60% of the activity period, almost irrespective of

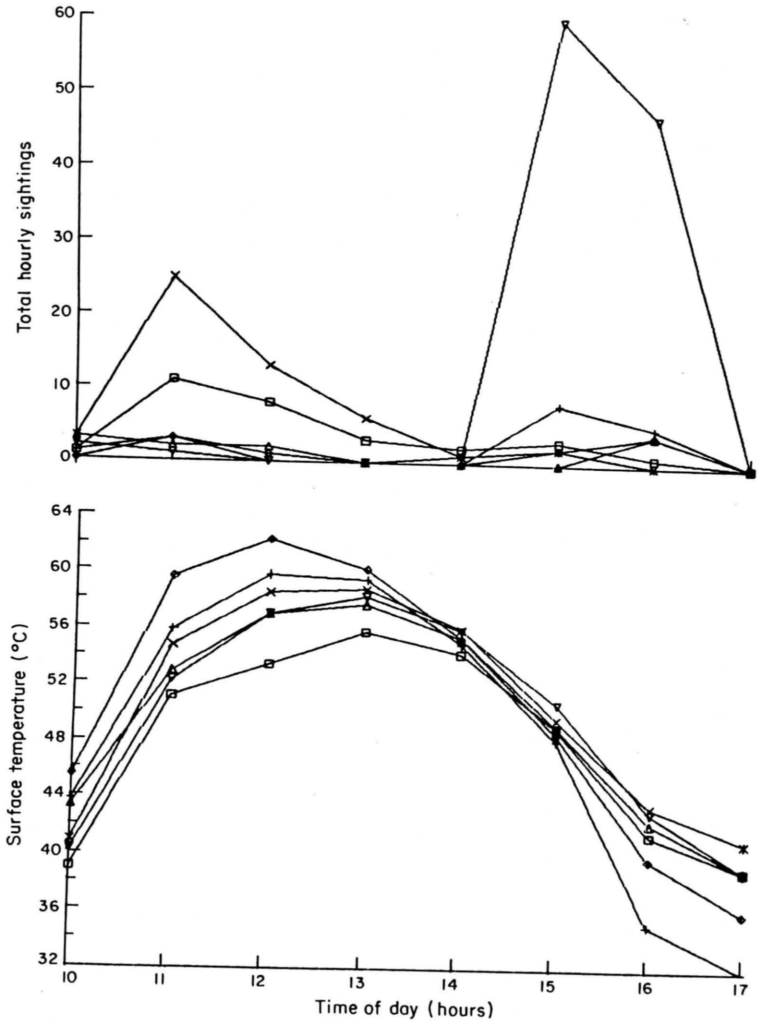

Figure 3 (*a*). Plot of hourly average surface temperatures and total hourly sightings of *Angolosaurus* for diurnal activity period 14 February □, Top; X, crest; +, lower slipface; ◇, middle slipface; △, upper slipface, ▽, avalanche base.

surface temperature. Emergence on the 17 February 1986 (Fig. 3*b*) was again between 10:00 and 11:00 local time. Again there was little correspondence between the onset of surface activity and occupancy of that portion of the dune, in this case the avalanche base, which might be expected to provide maximum rates of heating. If anything, it appeared that individuals were tending toward microsite locations on the dune that would tend to minimize heating rates throughout most of the active period. Finally, on 18 February 1986 (Fig. 3*c*), the day exhibiting the most uniform surface temperatures across the dune, *Angolosaurus* emergence occurred between 09:00 and 10:00. Once again, the correspondence between surface activity and the thermal mosaic appeared minimal with respect to maximizing an increase in body temperature.

Additional support for the apparent independence between environmental temperature and microsite choice above comes from statistical examination of the concordances of

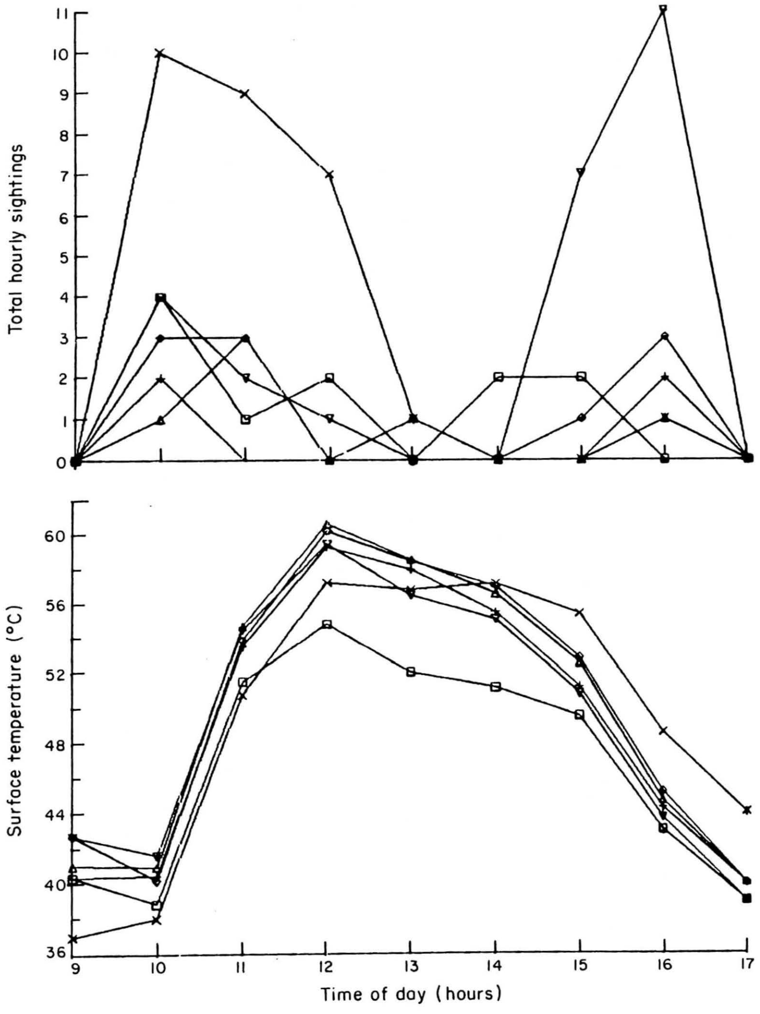

Figure 3(*b*). Plan of mean hourly surface temperature and total hourly sightings of *Angolosaurus* for diurnal activity period 17 February. See legend to Fig. 3(*a*).

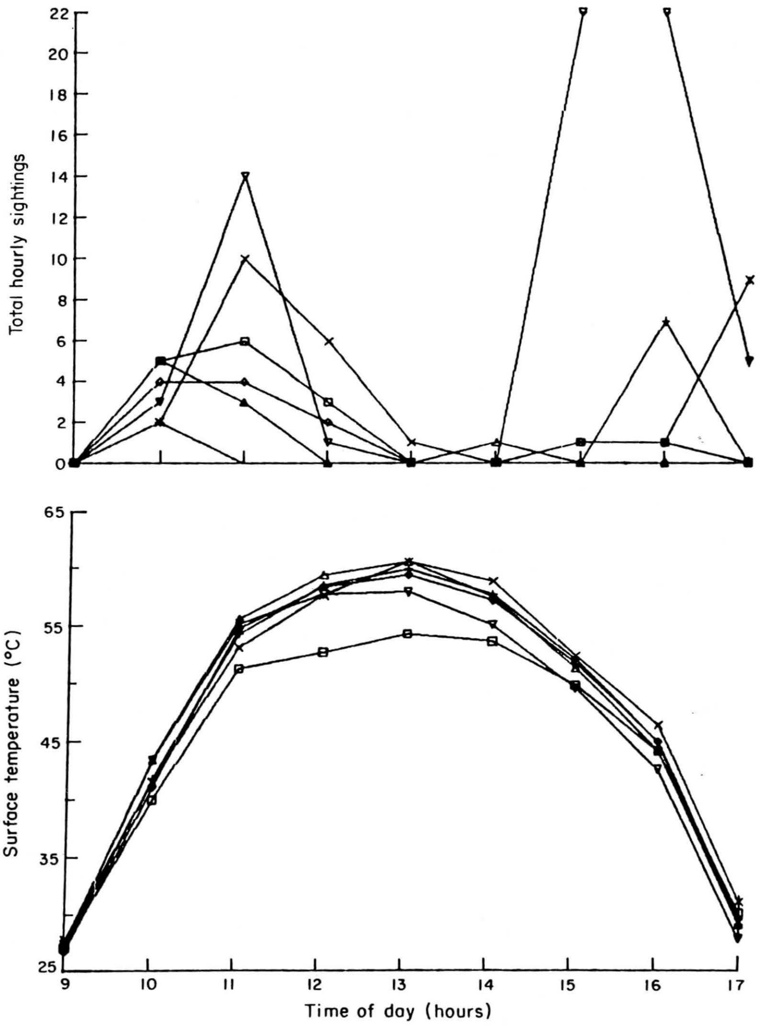

Figure 3(*c*). Plot of hourly average surface temperature and total hourly sightings of *Angolosaurus* for diurnal activity period 18 February. See legend to Fig. 3(*a*).

surface temperatures after emergence and patterns of habitat occupancy during the same period. Average surface temperatures during the first hour after emergence exhibited a high degree of concordance over the entire 7-day period of observation (Kendall's $W = 0{\cdot}618$, $n = 7$, $p < 0{\cdot}005$). This indicates that the pattern of surface heating of the dune is roughly the same each day despite minor variations. In contrast, total counts of *Angolosaurus* during the same time exhibit substantially lower daily concordance ($W = 0{\cdot}334$, $n = 7$, $p < 0{\cdot}05$) over the period of the study. That this measure is statistically significant indicates that a pattern of habitat occupancy at emergence is present, but that is it prone to considerable day-to-day variations. The large difference in these measures also suggests that the daily patterns seen for lizards may have little to do with surface temperatures across the dune. This is further evidenced by the almost complete absence of significant correlation between surface temperatures and the number of *Angolosaurus* in each activity area on any day during the period of obsefvation (Table 3).

Table 3. *Spearman rank correlations between average surface temperatures and total counts of active* Angolosaurus *in the seven activity areas across the dune during the first and third hours after emergence and during peak hour of afternoon activity. Values are correlation coefficients.*

Day	1st hour	3rd hour	Peak
1	0·345	0·089	0·345
2	0·319	−0·255	0·017
3	−0·357	−0·730*	0·473
4	−0·218	−0·571	0·741*
5	0·142	0·218	0·183
6	0·039	0·060	0·327
7	0·613	0·018	−0·306

* $p < 0{\cdot}05$; $n = 7$ for all days; minimum r_s necessary for significance $= 0{\cdot}679$.

These summaries reflect what is typically found of *Angolosaurus* activity (Seely *et al.*, 1988a; Mitchell *et al.*, 1988). Nonetheless, it is possible that the relationships between microsite occupancy on the dune and surface temperature are masked by the relatively large size and hence large thermal inertia of older individuals. If so, then thermal relationships should be more clearly apparent in the smaller size classes of *Angolosaurus*.

One of the clearest and most striking patterns forthcoming during these observations was that young *Angolosaurus* (6–10 g body mass) appeared to preferentially occupy the avalanche base region of the dune. Indeed, the relationship between the hourly totals of lizards active at the avalanche base and the number of young active was exceedingly tight over the period of the study ($y = 2{\cdot}77 + 0{\cdot}993\,x, r = 0{\cdot}970, n = 60, p < 0{\cdot}0001$) indicating that it was primarily young individuals who occupied this location. Yet, the curvilinear least squares regression between average surface temperatures and total hourly activity at the avalanche base ($y = -208{\cdot}16 + 10{\cdot}20x - 0{\cdot}11x^2, n = 60$; Fig. 4) explained only 13·6% of the total variation in surface activity. Thus, while statistically significant ($p = 0{\cdot}03$), the relationship is not of overrriding importance biologically. Notably, a very similar set of results is obtained for adults occupying the dune crest. Overall activity on the dune crest was strongly correlated with the number of adults active ($r = 0{\cdot}838, p < 0{\cdot}001$), yet the curvilinear regression relating activity on the crest to surface temperature ($y = -66{\cdot}18 + 3{\cdot}05x - 0{\cdot}029x^2, n{=}60$) explained little of the total variation in activity at that location ($r^2 = 0.130, p < 0{\cdot}02$).

On the whole, these data do not support the predictions from the maxithermy hypothesis with respect to thermal microhabitat selection. Indeed, an equally plausible alternative to maxithermy for these animals is that once active, *Angolosaurus* use areas of the dune for reasons having little or nothing to do with temperature (e.g. feeding, social interactions, predator surveillance), and continue to occupy such areas until body temperatures become unacceptably high. That the activity of young *Angolosaurus* at the avalanche base of the dune is primarily associated with foraging (Pietruszka *et al.*, 1986) provides support for this alternative view. Foraging in these individuals occurs at a time and dune location when the windblown seeds and other small bits of detritus on which they feed are readily available. On the dunes in the Unjab River region detritus accumulates on the leeward sides in response to surface winds, which are often substantial during the afternoon hours. Thus, the afternoon peaks of *Angolosaurus* activity seen at the avalanche base (Figs 3*a-c*) are not surprising.

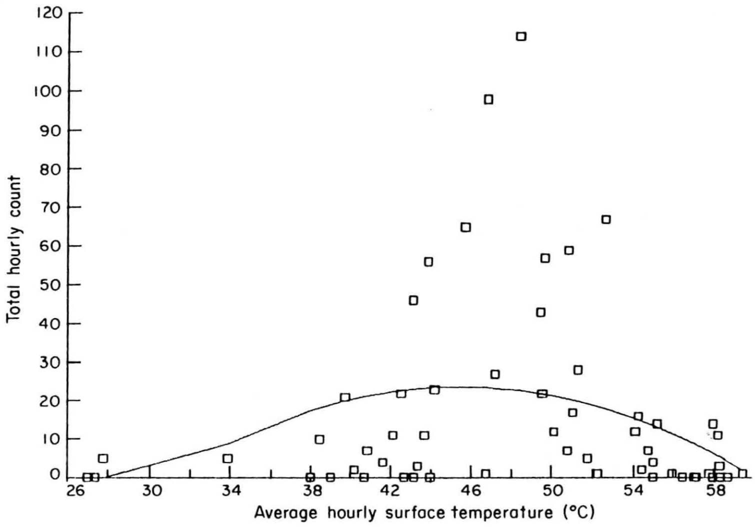

Figure 4. Least squares second-order polynomial regression of mean hourly surface temperature against total hourly counts of *Angolosaurus* on the avalanche base region of the dune. Although significant ($p = 0{\cdot}03$), $<14\%$ of the total variation in *Angolosaurus* at this microsite location was explained by surface temperature.

Subsurface sand provides an immediate and effective thermal refuge from excessively high surface temperatures (Louw & Seely, 1982; Seely *et al.*, 1988b) that is well within reach of *Angolosaurus*. Indeed, at a depth of 30 cm, sand temperature may be more than 20°C lower than it is on the surface. The presence of such a refuge provides the necessary ingredient for using the surface envionment in ways that need not be strongly coupled to temperature.

Ultimately, detailed measurements of body temperature may be necessary to distinguish between these alternative views of *Angolosaurus* thermal relations. However, the ecological patterns unveiled in the present study are similar to those found by Seely *et al.* (1988a) and strongly suggest that these animals are not maxitherms. Rather, they, like other ectothermic inhabitants of the Namib (Seely *et al.*, 1988b), appear exceedingly opportunistic in their use of thermal and other components of the sand dune habitat.

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